Mensural Discrimination of Four Species of *Peromyscus* (Rodentia: Muridae) in the Southeastern United States

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ABSTRACT—We subjected 17 mensural characters from a total of 460 cotton mice (*Peromyscus gossypinus*), white-footed mice (*P. leucopus*), deer mice (*P. maniculatus*), and old-field mice (*P. polionotus*) to discriminant analysis to maximally distinguish among specimens of these species in the southeastern United States. If external measurements are available, 13 characters are necessary to correctly classify all specimens. If external measurements are not available, 14 cranial characters discriminate at most 91% of the specimens. In pairwise comparisons using external and skull measurements, at least 98% of specimens can be separated with one or two characters. In pairwise comparisons (except *P. leucopus–P. maniculatus*) using only skull measurements, at least 95% of specimens can be correctly identified to species with one or two characters. For *P. leucopus* and *P. maniculatus*, six characters correctly separate 86% of the specimens, and two characters separate 82%.

White-footed mice (*Peromyscus*, Golger) are among the most widely distributed and ubiquitous North American mammals (Hall 1981), are the most broadly studied native mammals (King 1968), and are represented extensively in systematic collections. Despite their commonness and familiarity to most biologists, it is still difficult to distinguish among species when we use morphological characters (Hooper 1968). Much literature has resulted from regional attempts to provide for mensural discrimination among *Peromyscus*, especially between and within Osgood's (1909) *maniculatus* and *leucopus* species-groups. Papers have been published separating the white-footed mouse (*P. leucopus* [Rafinesque]), from the deer mouse (*P. maniculatus* [Wagner]) in New England (Choate 1973), Kansas (Choate et al. 1979), Wisconsin (Stromberg 1979), and Maryland (Feldhamer et al. 1983); separating the white-footed mouse from the cotton mouse (*P. gossypinus* [Le Conte]), in Alabama (Linzey et al. 1976) and eastern Texas (Engstrom et al.

1982); separating five *Peromyscus* species in New Mexico (Smart 1978); and separating four *Peromyscus* species in Arkansas (McDaniel et al. 1983). These studies indicate that it is usually possible to distinguish between morphologically similar species, but the characters necessary to do so vary geographically. Thus, for example, the characters used to distinguish between *P. leucopus* and *P. maniculatus* in New England differ from those in Wisconsin or Kansas. This almost ad hoc approach

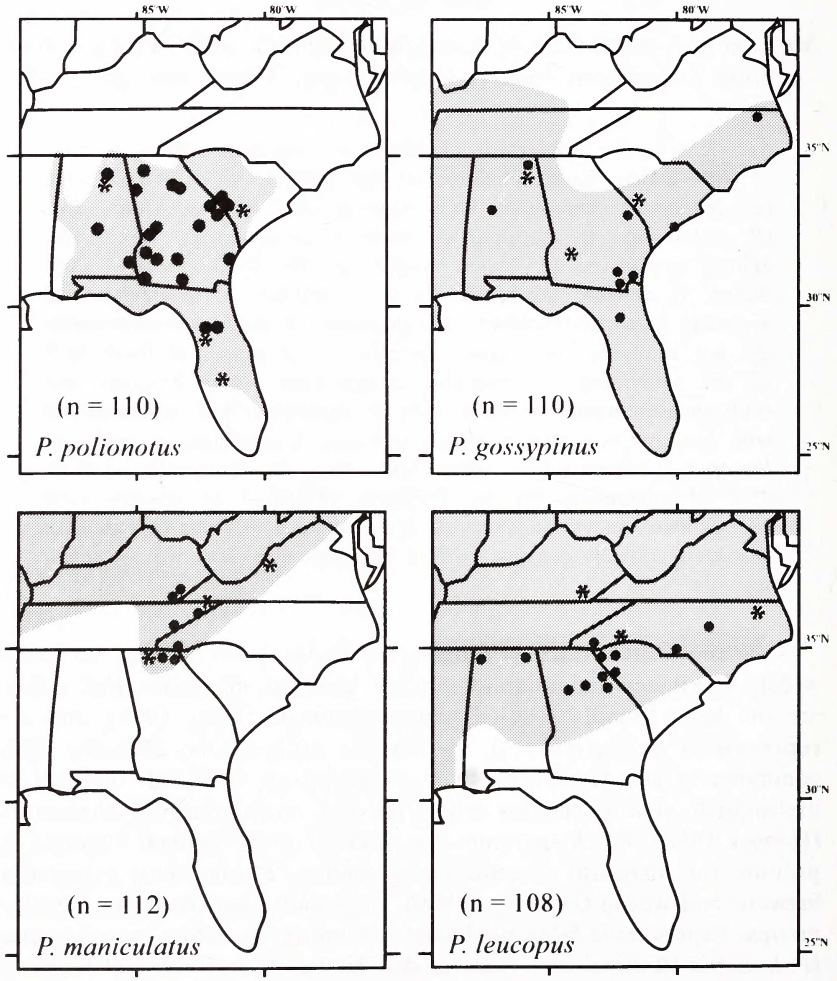

Fig. 1. Southeastern distribution of the four *Peromyscus* species showing collection location of the specimens used to build the model (•) and specimens used to test the model (*).

to the problem has been necessary because several of the species, particularly *P. leucopus* and *P. maniculatus*, have a high degree of intraspecific variation in morphology.

In the southeastern United States the ranges of four species overlap (Fig. 1). It is difficult to correctly identify these species using available taxonomic keys (e.g., Golley 1962, 1966; Blair et al. 1968; Hall 1981) based only on pelage features and/or cranial measurements. The four species usually can be distinguished based on collection location, habitat, and morphological data. Populations of *Peromyscus maniculatus* in this region are referred to as *P. m. nubiterrae* and are typically found in mesic forests at elevations higher than 900 m, and *P. maniculatus* usually has a sharply bicolored tail that is longer than the head and body. *Peromyscus gossypinus* is generally found in hardwood river bottoms and coastal oak-palmetto (*Quercus* sp. and *Serenoa repens*) forests and is the largest and heaviest of the four species. *Peromyscus polionotus* is generally found in areas of sandy soil and has a very short, distinctly bicolored tail. *Peromyscus leucopus leucopus* is generally found at elevations below 900 m in relatively xeric woodlands. Its tail is shorter than the head and body, and it is smaller and lighter in mass than *P. gossypinus*. A plot of principal component scores generated from the correlation structure of three standard external measurements (body, tail, and hind foot lengths) illustrates the overlap in measurements from specimens collected in the Southeast and graphically illustrates the difficulty in separating these four species based on these features (Fig. 2).

For museum personnel that acquire poorly curated public or private collections, or who desire to reexamine their holdings, identification of specimens from regions where ranges overlap may be difficult. The objective of this study is to examine the effectiveness of statistical procedures to distinguish these species in the southeastern United States without the use of collection-location information and without using statistically unsound ratios (Humphries et al. 1981). To do this, we generate discriminant functions from both external and skull measurements and from skull measurements alone.

METHODS

We used univariate and multivariate statistics to examine 460 *Peromyscus* museum specimens collected in the southeastern United States for variation in 17 morphometric characters. We selected sample sites based on the availability of large numbers of adult specimens from throughout the region. Sample sites were selected to reduce potential for incorrect a priori species identification by eliminating, to some degree, consideration of localities where ranges overlap. These criteria resulted in the distribution of sample sites in Figure 1.

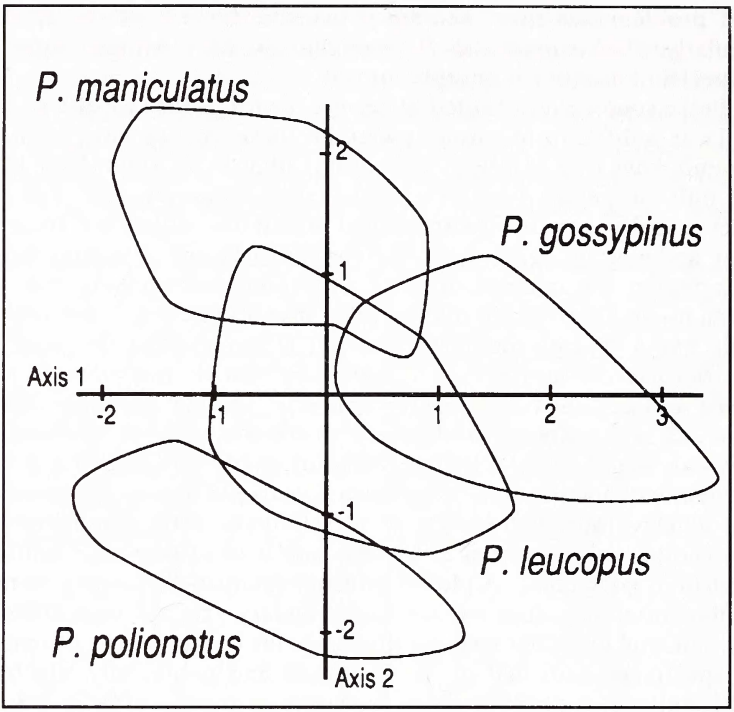

Fig. 2. Distribution of principal component scores generated from external measurements (body, tail, and hind foot lengths) illustrating overlap in the measurements of these characters.

A priori identifications were based on specimen tag information. We used only specimens we believed were correctly identified. We wanted to create a robust generalized model, but we also wanted to build the model based on, as much as possible, animals that we felt were correctly identified. The selection procedure resulted in using 110 *P. gossypinus*, 108 *P. leucopus*, 112 *P. maniculatus*, and 110 *P. polionotus*. The Appendix lists specimens examined. We used five additional specimens of each species, generally selected from locations not included in the model building process, to test the model.

One of us (JL) measured 14 cranial characters to the nearest 0.1 mm with dial calipers and recorded three external measurements from specimen tags. We estimated age from pelage characters (no juvenile gray), tooth wear (significant wear on all major cusps), and degree of cranial suture fusion. We measured only adults (in age classes 4–6 of Schmidly 1973) and excluded specimens with missing data from all analyses. Mensural characters (Choate et al. 1973, DeBlase and Martin

1981) included: head and body length (body), tail length (tail), hind foot length (foot), greatest skull length (SL), basonasal length (BNL), rostral breadth (RB), nasal length (NL), interorbital constriction (OC), zygomatic breadth (ZB), bony palate length (PL), maxillary toothrow length (MTL), total toothrow length (TTL), palatal width (PW), pterygoid breadth (PB), bullar depth (BD), and anterior palatal (incisive) foramen length (PFL). We measured rostral length (RL) from the anteriormost point of the nasals to the anterior edge of the zygomatic arch. Body length was calculated as the difference between total and tail lengths. We excluded ear length due to predominance of missing data.

We performed statistical analyses with Systat 5.1a (Wilkenson 1989) and SPSS 4.01 (Norusis 1990). We tested normality and homogeneity of variance by inspecting plotted residuals and by Bartlett's test for homogeneity of group variances, respectively. Differences among adult age classes and between sexes were tested with analysis of variance, and type I error rates were corrected with the Bonferroni adjustment (Rice 1989). We classified taxa using stepwise discriminant analysis. Variables were included in the models based on minimizing residual variance, prior probabilities were equal to sample size, and varimax rotation was employed. Stepwise discriminant analysis will find an optimal solution based on the data; however, depending on where the analysis begins (i.e., which variables enter the model first), it may find a local, rather than the global, optimum. To help avoid this optimization problem, we removed variables that entered the model in the first steps and repeated the analysis. In one case, that of discrimination based on all external and skull measurements, we found that bullar depth (BD) forced the model onto a local optimum. Therefore, we eliminated this character from further consideration in that model. We used stepwise discriminant analysis to produce two main predictive functions from the smallest set of characters needed to separate all four species—one for external and skull measurements and another for skull measurements alone. In addition, we generated predictive functions that used only one or two measurements to separate in pairwise comparisons among species.

We performed all analyses on raw data without transformation (because transformation did not result in homogeneous variances) and without removing size (Burnaby 1966, Rohlf and Bookstein 1987) because this produced the simplest tool for the identification of questionable specimens in the future. Although there was significant heterogeneity of variances among species for some characters, standard transformations (e.g., logarithm, etc.) did not homogenize it, and raw data were more effective in discrimination than log-transformed data.

Table 1. Mean, standard error, and range of 17 external and cranial measurements (mm) of four *Peromyscus* species in the southeastern United States.

Character	*P. gossypinus*			*P. leucopus*			*P. maniculatus*			*P. polionotus*		
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Body	99.5	0.74	82–133	87.6	0.65	73–106	86.3	0.68	71–102	75.7	0.62	59–99
Tail	73.1	0.58	58–91	65.1	0.66	49–83	88.3	0.68	71–106	45.1	0.37	36–53
Foot	22.1	0.09	20–24	19.4	0.09	16–21	20.1	0.10	16–22	16.8	0.10	13–20
Greatest skull length (SL)	27.9	0.09	25.8–29.9	25.2	0.07	23.0–27.1	24.6	0.07	22.8–27.0	22.2	0.07	20.1–23.9
Basonasal length (BNL)	25.2	0.10	22.6–28.4	22.6	0.08	20.7–24.4	22.0	0.07	20.0–23.7	19.8	0.07	17.5–21.6
Rostral length (RL)	9.0	0.05	7.8–10.4	7.6	0.03	26.8–8.5	7.7	0.04	6.6–8.8	6.8	0.04	5.8–7.8
Greatest rostral breadth (RB)	3.2	0.02	2.8–3.6	3.0	0.02	2.6–3.4(3.8)[1]	2.9	0.02	2.5–3.3	2.8	0.02	2.4–3.1(3.7)
Nasal length (NL)	11.0	0.06	9.5–12.2	9.7	0.05	8.5–11.0	9.6	0.04	8.3–10.5	8.6	0.05	7.4–9.5
Interorbital constriction (OC)	4.4	0.01	4.0–4.7	4.1	0.02	3.7–4.7	3.9	0.02	3.2(2.8)–4.4	3.7	0.02	3.3–4.1(4.8)
Zygomatic breadth (ZB)	14.1	0.06	12.9–15.7	12.9	0.04	12.0–13.9	12.6	0.04	11.6–13.8	11.7	0.04	10.8–12.7
Bony palate length (Palatilar) (PL)	11.1	0.05	9.9–12.6	9.9	0.04	8.9 10.8	9.7	0.03	8.8–10.7	8.7	0.04	7.4–9.9
Maxillary toothrow length (MTL)	3.8	0.02	3.4–4.1	3.4	0.02	3.0–3.8	3.4	0.01	3.1–3.9	3.1	0.02	2.6–3.5
Total toothrow length (TTL)	12.7	0.04	11.7–13.7	11.5	0.03	10.5–12.3	11.2	0.03	10.4–12.1	10.1	0.03	9.3–10.8
Palatal width (PW)	3.0	0.01	2.7–3.3	2.7	0.02	2.4–3.1	2.6	0.01	2.3–3.0	2.5	0.01	2.2–2.9
Pteryogoid breadth (PB)	1.5	0.02	1.0–1.7	1.3	0.01	0.8–1.6	1.2	0.01	1.0–1.5	1.2	0.01	1.0–1.4(1.5)
Bullar depth (depth of skull) (BD)	9.5	0.03	8.5–10.3	8.8	0.03	8.1–9.6	8.4	0.03	7.8–9.0	8.1	0.03	7.4–8.9
Ant. palatal foramen length (PFL)	5.6	0.03	4.7–6.3	4.7	0.03	4.0–5.4	4.7	0.02	3.9–5.2	4.1	0.02	3.6–4.7

[1] Extreme measurements, those greater than five standard deviations from the mean, are shown in parentheses.

RESULTS

In univariate tests, we found significant differences between the sexes in *P. gossypinus* for body length ($P \leq 0.02$), RL ($P \leq 0.02$), and NL ($P \leq 0.05$); in *P. leucopus* for foot ($P \leq 0.03$) and PFL ($P \leq 0.04$); in *P. maniculatus* for SL ($P \leq 0.05$), PB ($P \leq 0.04$), and PFL ($P \leq 0.01$); and in *P. polionotus* for body length ($P \leq 0.01$). Although these differences were individually significant, there was considerable overlap in character ranges, and none was significant when we applied the Bonferroni correction (table-wide significance began at $P \leq 0.003$). The differences between the sexes of *P. maniculatus* approached significance ($P \leq 0.07$), but none was significantly different ($P \leq 0.05$) when subjected to two group (i.e., male vs. female) discriminant analysis. We included gender in the discriminant analysis of all characters, but its effect was not significant, and it did not enter the final stepwise model. Table 1 contains means, ranges, and standard errors for all characters.

Univariate analyses were marginally successful in identifying the four species, but no single measurement unambiguously separated them. Most characters separated the large *P. gossypinus* from the small *P. polionotus*, but six of 17 characters showed overlapping distributions. Tail length greater or less than 55 mm is the simplest method to separate these two species. No single character could separate *P. gossypinus* from *P. leucopus* or *P. maniculatus*, but anterior palatal foramen length 5.4 mm identified most (67%) *P. gossypinus*. Tail length 83 mm separated 81% of *P. maniculatus* from the other three species, but four *P. gossypinus* had tails longer than 83 mm. There was no overlap in the tail lengths of *P. polionotus* and *P. maniculatus*. No single character separated *P. leucopus* from *P. maniculatus*.

Multivariate analyses using external and skull measurements were successful in identifying the four species. Stepwise discriminant analysis correctly classified all specimens using measurements of 13 characters (in order of inclusion into model: Tail, SL, MTL, Foot, RL, OC, PFL, Body, TTL, PB, BNL, PL, PW). The three axes accounted for 55.51, 37.16, and 7.34% of the variance (Fig. 3*a*). After a varimax rotation, the variables most highly correlated with the first discriminant function were TTL (0.87), SL (0.85), BNL (0.74), PL (0.69), RL (0.58), PFL (0.58), ZB (0.57), MTL (0.53), and NL (0.52); those highly correlated with the second function were BD (0.82), PB (0.40), and OC (0.37); and those highly correlated with the third function were PFL (0.49), RL (0.45), PB (0.23), and OC (-0.21).

Discriminant analysis using only skull measurements correctly classified at most 90% of the specimens with 10 characters (in order of inclusion into model: SL, BD, MTL, RL, PFL, OC, TTL, BNL, PB,

Table 2. Unstandardized discriminant function coefficients using one or two morphological characters of four *Peromyscus* species in the southeastern United States. Each cell contains characters used, coefficients, constants, and numbers of errors for each set of species. Discriminant scores for each pair of species have opposite signs, and this is indicated as one species greater than zero. Cells above the diagonal are skull only; cells below the diagonal are external and skull characters. Variables defined in the Methods.

	P. gossypinus	*P. leucopus*	*P. maniculatus*	*P. polionotus*
P. gossypinus		SL 0.927 MTL 3.732 C -32.229 Pg scores > 0 Errors: P1 2; Pg2	SL 0.794 BD 2.123 C -39.78 Pg scores > 0 Errors: none	SL 1 C -25 Pg scores > 0 Errors: none
P. leucopus	Foot 0.593 SL 0.821 C -34.125 Pg scores > 0 Errors: Pg 5; Pl 1		OC 2.523 BD 2.754 C -33.762 Pl scores > 0 Errors: Pm 15: Pl 24	SL 1.214 MTL 2.636 C -37.389 Pl scores > 0 Errors: Pp 1; Pl 2
P. maniculatus	BNL 0.685 BD 2.403 C -37.611 Pg scores > 0 Errors: Pg 1; Pm 0	Tail 0.165 BNL -1.028 C 10.271 Pm scores > 0 Errors: Pl 0; Pm 1		SL 0.68 TTL 1.803 C -35.126 Pm scores >0 Errors: Pp 4; Pm 8
P. polionotus	Tail 1 C -55 Pg scores > 0 Errors: none	Tail 0.085 SL 0.953 C -27.251 Pl scores > 0 Errors: Pl 3; Pp 0	Tail 1 C -60 Pm scores > 0 Errors: none	

PW). After a varimax rotation, the variables most highly correlated with the first discriminant function were SL (0.74), TTL (0.74), BNL (0.66), PFL (0.66), RL (0.65), PL (0.62), Foot (0.59), MTL (0.53), ZB (0.53), and NL (0.50); the only variable highly correlated with the second function was Tail (0.82, all others were less than ±0.17); at -0.33, OC was most highly correlated with the third function. All the misclassifications of the data were in separating *P. leucopus* and *P. maniculatus* (Fig. 3*b*). This observation led us to implement a two-step discrimination process as suggested by Thompson and Conley (1983). First, we grouped *P. leucopus* and *P. maniculatus* and performed discriminant analysis among *P. gossypinus*, *P. polionotus*, and *P. leucopus-P. maniculatus*; then we separated *P. leucopus* and *P. maniculatus*. However, this scheme did not improve the classification results.

In analysis of species pairs, at least 98% of specimens could be separated using only one or two external and/or skull measurements (Table 2). In pairwise comparisons using only skull measurements, we could separate at least 95% of the specimens (except for *P. leucopus–P. maniculatus*). For this species pair two characters separate 82% of the specimens. The scores generated by the discriminant functions (Table 2) approximately fall on either side of zero, such that scores for one species are positive, and scores for the other species are negative. However, these models do generate a few misclassifications; therefore, specimens with scores near zero (e.g., ±0.5) should be subjected to the full discriminant models.

DISCUSSION

Discrimination of these *Peromyscus* species is difficult when collection location information or skins are missing, and we did not achieve the ultimate goal of this project which was to correctly classify any skull without external information. However, the great majority of specimens can be correctly assigned to species, and the discriminant function was useful in identifying likely misclassified and questionable specimens in our museum collections. Additionally, the function allows evaluation of specimens collected at the periphery of species' ranges.

The model using external and skull characters was reasonably successful in classifying the test specimens, which suggests that we captured enough of the variation within each species to make it useful in classifying specimens from somewhat beyond the geographic distribution of our samples. This is an improvement over the ad hoc approach where each state or region requires a different discrimination model. However, although the *P. maniculatus* test specimens classified correctly, they tended to fall in the margins of the discriminant score distributions. The model with only skull measurements was less successful in classifying

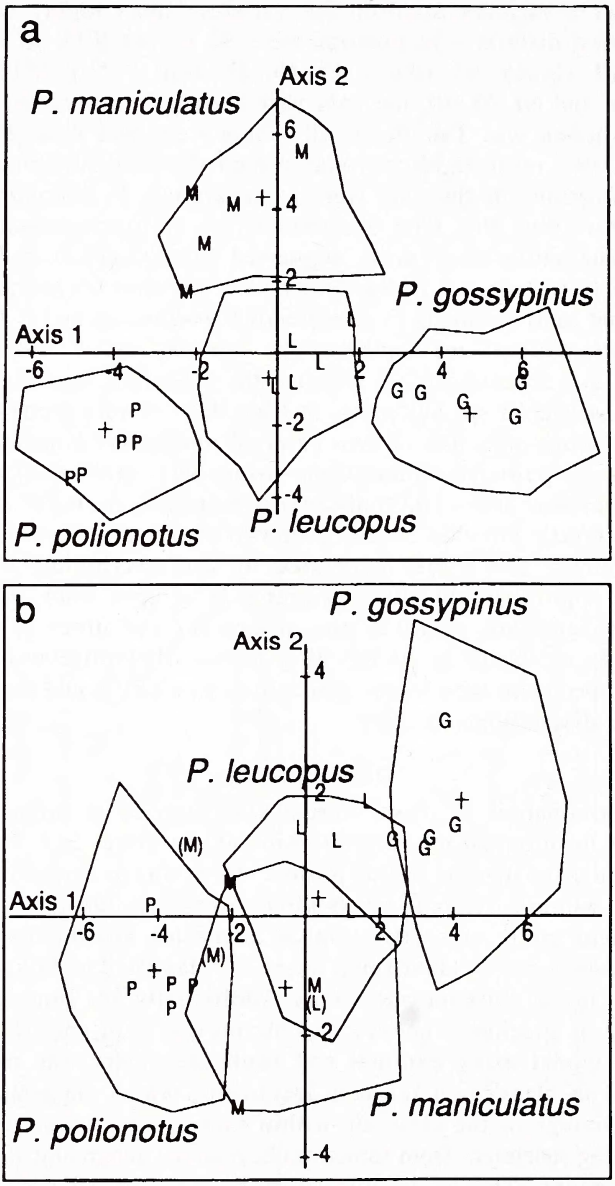

Fig. 3. Distribution of discriminant scores generated from (a) external and skull measurements and from (b) skull measurements alone plotted on the first two canonical axes. Letters (the first letter of the specific epithet for each species) designate the location of test specimens, letters in parentheses mark misclassifications, and crosses mark group centroids.

the test specimens, and results should be viewed with caution if that model is used for specimens collected far outside the geographic distribution of our samples.

Our results were similar to those of previous authors who found that these species tend to differ significantly in most measurements, but that there is generally some overlap in measurement that prevents classification of some specimens based on single characters. For example, Linzey et al. (1976) could separate most specimens using anterior palatal foramen length and width or skull length. Choate (1973) could separate most specimens with tail length. Engstrom et al. (1982) found that *P. gossypinus* differed significantly from *P. leucopus* in every character they measured, but that there was overlap in all characters. McCarley (1954) found that hindfoot length separated most *P. leucopus* from *P. gossypinus*.

Stromberg (1979) successfully used discriminant analysis on external characters to separate *P. maniculatus* from *P. leucopus*. We found that these characters could not be used in the extreme Southeast (Fig. 2). However, he found that ear length was especially useful, and we were not able to include that character. We disagree with Stromberg's (1979) statement that discrimination of external characters offers a dependable alternative to cranial measurements in the identification of *P. maniculatus* and *P. leucopus*. As in our study, McDaniel et al. (1983) and Choate et al. (1979) were able to separate almost all of their specimens using cranial measurements. Only Engstrom et al. (1982) was able to separate all of their specimens using cranial measurements.

Choate (1973), Choate et al. (1978), and Engstrom et al. (1982) found that variation among adult age classes was required in the models for accurate classification. In contrast, we did not find that age variation among adult age classes (4–6, Schmidly 1973) was significant. We found statistical differences among age classes 4–6, but these differences were small relative to the differences among species, and thus age information was not important in our models.

Several authors have found ratios useful in identifying *Peromyscus* species pairs. McDaniel et al. (1983) found that the ratio of interorbital width to length of the nasal bone was useful in separating *P. attwateri* from *P. gossypinus*. Feldhamer et al. (1983) found that the ratio of tail length to body length in conjunction with body mass separated *P. leucopus* from *P. maniculatus* (pregnant females excluded). McCarley (1954) used the ratio of skull length to foot length to identify *P. gossypinus*, *P. leucopus*, and their purported hybrids. Although ratios may provide useful indices, we agree with Humphries et al. (1981) and the references they provide that ratios should be avoided in morphometric

studies because of statistical and conceptual difficulties. Discriminant analysis based on two characters has a similar result of separating groups based on the magnitude of two measurements. It also has the benefits of potentially better separation of groups by stretching the axes (weighing measurements with discrimination function coefficients) and an associated probability of group membership. Therefore, we have presented results (Table 2) that use one or two measurements rather than ratios to separate pairs of species with discriminant functions.

We agree with Choate (1973) that habitat and external features (e.g., tail coloration, penciled tail, color, and degree of fur luxuriance) can yield important information for classifying these species. For example, we believe that the best ways to identify *P. polionotus* are that it is found on sandy soils and by its short, strongly bicolored tail, and the best ways to identify *P. leucopus* are that it is found in low elevation exeric sites and that it has more reddish-orange on the sides than *P. gossypinus*. Other qualitative characters may also be useful. For example, Linzey et al. (1976) found that the skulls of *P. leucopus* tend to be lighter and more fragile than those of *P. gossypinus*. However, our goal was to identify these species with quantitative characters rather than qualitative characters, and preferably with the skull alone, as noted by Feldhamer et al. (1983), these qualitative characteristics can be variable within species. Most of the classification problems we encountered involved old skulls without associated skins.

Use of the discriminant function—Discriminant analysis combines variables to generate a set of linear, independent axes upon which specimens, after appropriate scoring, can be plotted and their classification determined. The appropriate scoring method is to multiply each morphological character variable (e.g., foot length, skull length) by its discriminant function coefficient, sum the products, and add a constant (for each axis separately). In general:

$$D_1 = B_{10} + B_{11}X_1 + B_{12}X_2 + B_{13}X_3 + \ldots + B_{1n}X_n$$

$$D_2 = B_{20} + B_{21}X_1 + B_{22}X_2 + B_{23}X_3 + \ldots + B_{2n}X_n$$

where D_1 is the specimen's discriminant score on the first axis, the B_{1i}'s are discriminant function coefficients estimated from the data for the first axis (B_{i0}'s are constants), and the X_i's are the values of the original variables. This is done separately for each axis, and the scores, D_1, D_2, ..., D_n, form the coordinate of the specimen's location in the n-dimensional discriminant space. For example, to separate *P. gossypinus* from *P. leucopus* using external and skull measurements, the appropriate transformation is (only one axis is needed)

$$D = -34.125 + 0.593(\text{hindfoot length}) + 0.821(\text{skull length}).$$

Table 3. Unstandardized canonical discriminant function coefficients, external and skull characters, and skull characters only for four *Peromyscus* species in the southeastern United States.

	External and Skull			Skull Only		
Character	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Body	-0.009	-0.03	0.013			
Foot	0.366	-0.016	-0.008			
Tail	-0.002	0.194	0.005			
SL	0.633	-0.199	-1.295	1.13	-0.602	-0.944
BNL	-0.287	-0.38	-0.325	-0.465	0.782	-0.419
RL	0.443	0.043	2.687	-0.356	0.121	2.714
OC	0.511	-0.482	-1.636	0.393	1.055	-1.326
PL	-0.338	-0.151	0.058			
MTL	2.041	-0.461	0.434	2.016	0.31	1.219
TTL	0.567	0.355	-1.174	1.342	-1.551	-0.908
PW	-0.007	-0.764	0.995	-0.31	0.762	1.107
PB	1.11	-0.583	1.458	-0.365	2.57	1.766
BD				-0.074	2.958	-0.047
PBL	0.997	-0.298	2.225	0.298	-0.233	2.514
Constant	-37.36	8.115	20.128	-38.27	-21.09	6.454

Table 4. Group centroids for external and skull characters and for skull characters only based on unstandardized canonical discriminant function coefficients of four *Peromyscus* species in the southeastern United States.

	External and Skull Characters			Skull Characters Only		
Species	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
P. gossypinus	4.710	-1.654	-0.811	4.309	1.915	0.817
P. leucopus	-0.099	-0.671	-1.337	0.356	0.308	-1.261
P. maniculatus	-0.354	4.328	0.491	-0.528	-1.196	0.164
P. polionotus	-4.209	-2.108	1.616	-4.121	-1.000	0.255

Given an unknown specimen with hindfoot and skull lengths of 23.5 and 28.7 mm, respectively, and the coefficients of these measurements from Table 3, this equation becomes:

$$D = -34.125 + 0.593(23.5) + 0.821(28.7)$$

$$D = 3.377$$

In this case, any positive value of D indicates *P. gossypinus*, and any negative value of D indicates a *P. leucopus* (Table 2). Thus, this specimen is a *P. gossypinus*.

If these two species required more than one axis, D_1 and D_2 would be calculated using discriminant coefficients from Table 3 for external and cranial measurements or Table 4 for skull measurements only. The bivariate coordinate (D_1, D_2) can be plotted on a 2-dimensional graph (e.g., Fig. 3).

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LITERATURE CITED

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APPENDIX

Specimens examined to build the model.

Museum acronyms are defined in the acknowledgments. Location names are states and counties.

P. gossypinus—ALABAMA: Jackson; 9 USNM). Tuscaloosa; 7 (UAL). FLORIDA: Alachua; 13 (UF). GEORGIA: Burke; 12 (MCZ), 2 (USNM). Camden; 13 (UGAMNH). Charlton; 22 (UGAMNH). Ware; 8 (UGAMNH). NORTH CAROLINA: Gates; 8 (LSUMZ). SOUTH CAROLINA: Charleston; 16 (CMNH).

P. leucopus—ALABAMA: Colbert; 1 (USNM). Jackson; 4 (USNM). GEORGIA: Barrow; 1 (UGAMNH). Clarke; 40 (UGAMNH). Dekalb; 1 (UGAMNH). Elbert; 1 (UGAMNH). Oconee; 1 (UGAMNH). Rockdale; 1 (UGAMNH). Walton; 1 (UGAMNH). Wilkes: 1 (UGAMNH). NORTH CAROLINA: Anson; 3 (USNM). Jackson; 8 (USNM). Macon: 2 (UGAMNH). Wake; 7 (USNM). SOUTH CAROLINA: Abbeville; 1 (USNM). Greenville; 2 (USNM). Oconee; 7 (USNM). Pickens; 4 (USNM).

P. maniculatus—GEORGIA: Rabun; 9 (UGAMNH). Towns; 9 (UGAMNH). Union; 27 (UGAMNH). KENTUCKY: Bell; 7 (USNM). Harlan; 12 (USNM). NORTH CAROLINA: Macon; 21 (UGAMNH). TENNESSEE: Carter, 9 (USNM). Johnson; 2 (USNM). Sevier; 16 (USNM).

P. polionotus—ALABAMA: Autauga; 7 (USNM). Henry; 7 USNM). Marshall; 1 (USNM). FLORIDA: Indian River, 5 (UGAMNH). Marion; 5 (UGAMNH). GEORGIA: Baker, 2 (UGAMNH). Barrow; 2 (UGAMNH). Burke; 1 (UGAMNH). Clarke; 10 (UGAMNH). Decatur; 3 (UF). Dougherty; 2 (USNM). Gordon; 3 (USNM). Haralson; 3 (UGAMNH). Irwin; 2 (UF). Johnson; 2 (UGAMNH). Lowndes; 2 (UGAMNH). Marion; 1 (UF). McIntosh; 3 (UGAMNH). Randolph; 10 (UGAMNH). Richmond; 2 (UGAMNH). Seminole; 2 (UF). Taylor; 1 (USNM). Tift; 13 (USNM). SOUTH CAROLINA: Aiken; 12 (UGAMNH). Barnwell; 9 (UGAMNH).

Specimens examined to test the model.

P. gossypinus—ALABAMA: Dekalb; 2 (UI). GEORGIA: Dougherty; 2 (UI). SOUTH CAROLINA: Aiken; 1 (UGAMNH).

P. leucopus—KENTUCKY: Bell; 1 (UGAMNH). NORTH CAROLINA: Gates; 2 (UGAMNH). McDowell; 2 (UGAMNH).

P. maniculatus—GEORGIA: Fannin; 2 (UGAMNH). NORTH CAROLINA: Watauga; 1 (USNM). TENNESSEE: Carter; 1 (UGAMNH). VIRGINIA Giles; 1 (UGAMNH).

P. polionotus—ALABAMA: Marshall; 1 (USNM). FLORIDA: Highlands; 2 (UGAMNH). Marion; 1 (UGAMNH). SOUTH CAROLINA: Barnwell; 1 (UGAMNH).